

# The role of temperature in determining the stimulation of CO<sub>2</sub> assimilation at elevated carbon dioxide concentration in soybean seedlings

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Soybean (*Glycine max* cv. Clark) was grown at both ambient (ca 350  $\mu\text{mol mol}^{-1}$ ) and elevated (ca 700  $\mu\text{mol mol}^{-1}$ ) CO<sub>2</sub> concentration at 5 growth temperatures (constant day/night temperatures of 20, 25, 30, 35 and 40°C) for 17–22 days after sowing to determine the interaction between temperature and CO<sub>2</sub> concentration on photosynthesis (measured as A, the rate of CO<sub>2</sub> assimilation per unit leaf area) at both the single leaf and whole plant level. Single leaves of soybean demonstrated increasingly greater stimulation of A at elevated CO<sub>2</sub> as temperature increased from 25 to 35°C (i.e. optimal growth rates). At 40°C, primary leaves failed to develop and plants eventually died. In contrast, for both whole plant A and total biomass production, increasing temperature resulted in less stimulation by elevated CO<sub>2</sub> concentration. For whole plants, increased CO<sub>2</sub> stimulated leaf area more as growth temperature increased. Differences between the response of A to elevated CO<sub>2</sub> for single leaves and whole plants may be related to increased self-shading experienced by whole plants at elevated CO<sub>2</sub> as temperature increased. Results from the present study suggest that self-shading could limit the response of CO<sub>2</sub> assimilation rate and the growth response of soybean plants if temperature and CO<sub>2</sub> increase concurrently, and illustrate that light may be an important consideration in predicting the relative stimulation of photosynthesis by elevated CO<sub>2</sub> at the whole plant level.

**Key words** – Acclimation, elevated CO<sub>2</sub>, feedback inhibition, *Glycine max*, leaf area index, self-shading, soybean.

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## Introduction

It is well known that atmospheric CO<sub>2</sub> is increasing and is expected to exceed 600  $\mu\text{mol mol}^{-1}$  by the end of the 21st century (Schlesinger 1986). While short-term (i.e. minutes, hours) exposure to elevated CO<sub>2</sub> increases net photosynthesis in leaves of plants possessing C<sub>3</sub> metabolism, the same leaves exposed to long-term (days, weeks) concentrations of elevated CO<sub>2</sub> may not always show continued photosynthetic stimulation relative to the ambient CO<sub>2</sub> condition. This increasing insensitivity of photosynthesis to elevated CO<sub>2</sub> concentrations has been observed in a large number of studies for a wide range of experimental conditions (cf. Wulff and Strain 1982, Cure

and Acock 1986, Sicher et al. 1994). In contrast, a few studies have shown continued stimulation of photosynthesis (determined as CO<sub>2</sub> assimilation) at elevated CO<sub>2</sub> for months or years (Ziska et al. 1990, Eamus et al. 1993). Since plant productivity can be determined in large part by photosynthetic rate, it will become critical to understand those factors which influence the degree of photosynthetic stimulation as atmospheric CO<sub>2</sub> increases (cf. Bunce and Ward 1986, Sage 1994, Woodrow 1994).

One such potential factor is the predicted increase in global temperature. It is expected that the increase in atmospheric CO<sub>2</sub> may result in a concurrent increase in the mean surface temperature of the earth (3–4 K with a doubling of current CO<sub>2</sub>, see Schlesinger 1986). Such an

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increase in mean temperature could also be accompanied by an increase in the frequency of extremely high temperature events (Mearns et al. 1984).

If the photosynthetic response of plants to CO<sub>2</sub> and temperature is interactive, then the temperature response at ambient CO<sub>2</sub> could not be used to predict the response at elevated CO<sub>2</sub>. When plants are first exposed to an elevated CO<sub>2</sub> environment, the net photosynthetic rate is stimulated. This is, in part, because high CO<sub>2</sub> concentration increases the velocity of carboxylation and reduces photorespiration (Long 1991). Since photorespiratory carbon loss increases with temperature, elevated CO<sub>2</sub> should stimulate net photosynthesis more as temperature rises (Long 1991, Potvin 1994). Observations of greater photosynthetic stimulation (as well as growth) at elevated CO<sub>2</sub> with increasing temperature are consistent with these theoretical predictions for a wide range of plant species (Idso et al. 1987, Sage and Sharkey 1987, Acock et al. 1990, Ziska et al. 1990).

One notable exception to the predicted interaction of temperature and CO<sub>2</sub> on photosynthesis and growth is soybean. To date, a number of studies have shown that the relative enhancement of CO<sub>2</sub> assimilation in soybean exposed to elevated CO<sub>2</sub> is unchanged (Jones et al. 1985, Campbell et al. 1990, Baker and Allen 1993) or even decreased with increasing temperature (Sionit et al. 1987). Presumably such a response is not a result of supra-optimal growth temperatures, since soybean is well adapted to tropical and subtropical conditions.

In our previous work with soybean, we observed that long-term enhancement of CO<sub>2</sub> assimilation by higher CO<sub>2</sub> concentrations and temperature differed between single leaves and whole plants (Ziska and Bunce 1995). This suggested that the relative enhancement of assimilation at high CO<sub>2</sub> and increased temperature could vary depending on the level of complexity examined (i.e. leaves vs whole plant); however, to date, no direct comparisons have been made. To quantify the response and to determine the basis for potential differences in long-term enhancement of CO<sub>2</sub> assimilation between single leaves and whole plants with elevated CO<sub>2</sub> at changing temperature, soybean was grown at five constant day/night temperatures (20, 25, 30, 35 and 40°C) and two CO<sub>2</sub> concentrations (350 and 700 µmol mol<sup>-1</sup>).

**Abbreviations** – A, CO<sub>2</sub> assimilation; DAS, days after sowing; LAI, leaf area index; LAR, leaf area ratio; NAR, net assimilation rate; RGR, relative growth rate; R/S, root shoot ratio.

## Materials and methods

Experiments were conducted in controlled environment chambers located at the Climate Stress Laboratory, USDA-ARS, Beltsville, Maryland, using soybean (*Glycine max* cv. Clark, maturity group IV). Seed for Clark was obtained from the USDA soybean germplasm collection in Urbana, Illinois.

For each controlled environment chamber (EGC, Chagrin Falls, OH, USA), the CO<sub>2</sub> concentration was

controlled by continuous flushing with CO<sub>2</sub>-free air, then re-injection with CO<sub>2</sub> to maintain the desired CO<sub>2</sub> concentration. Injection of CO<sub>2</sub> was controlled by an absolute infra-red gas analyzer (WMA-2, PP Systems, Haverhill, MA, USA) which sampled air continuously. The set points for CO<sub>2</sub> were 350 (ambient) and 700 µmol mol<sup>-1</sup> (elevated, 100% above ambient). Actual CO<sub>2</sub> concentrations for an average 24 h period were 356 ± 13 and 699 ± 2 µmol mol<sup>-1</sup>. Since only one pair of chambers was available, the same experiment was repeated five times at constant day/night temperatures of 20, 25, 30, 35 and 40°C ± 0.5°C. To determine the effect of a lower growth temperature on leaf initiation, the 35°C was repeated with a lower temperature (25°C) used for the period from sowing until unfolding of the first trifoliate leaf. In all experiments, plants received 14 h of 1 000 µmol m<sup>-2</sup> s<sup>-1</sup> photosynthetic photon flux density (PPFD) at the upper leaf level from a mixture of incandescent, high pressure sodium and metal halide lamps (GE Corp., Glen Ellen, VA, USA). At temperatures between 20 and 35°C, average daily relative humidity (RH) exceeded 60% (ca 65%); however, average daily RH for the 40°C growth temperature was 49%. Temperature, CO<sub>2</sub> concentration and RH were monitored and recorded at 1-min intervals by a EGC network datalogger (EGC Corp.) in conjunction with a PC.

Two to three seeds were sown in 15-cm diameter plastic pots filled with 1.8 l of vermiculite. All pots were thinned to one seedling within 2–3 days following emergence. For each experiment at a given growth temperature, 20 to 25 pots were assigned to each CO<sub>2</sub> treatment. Pots were arranged to avoid shading from other plants. All pots were watered daily (twice daily at the 35 and 40°C growth temperatures) with complete nutrient solution containing 13.5 mM nitrogen (Robinson 1984).

Measurement of 24-h whole plant gas exchange for each experiment began at the same physiological stage (unfolding of first trifoliate). Age at this physiological stage differed depending on growth temperature and CO<sub>2</sub> concentration. To determine daily rates of CO<sub>2</sub> assimilation, whole plants were placed inside one of two ca 5-l Mylar chambers held at the respective growth temperature. Air of the same CO<sub>2</sub> concentration used during growth was obtained by mixing CO<sub>2</sub>-free air with pure CO<sub>2</sub> before it passed through each chamber. The air stream was humidified by bubbling through a water-filled container. Humidity, light and temperature within the smaller measurement chamber were set to match those of the entire growth chamber. A differential infrared CO<sub>2</sub> analyzer (Li-Cor 6252, Lincoln, NE, USA) measured the net CO<sub>2</sub> exchange rate over a 7–9-day period across each of the smaller chambers. The sensitivity of the analyzer was corrected for the background CO<sub>2</sub> concentration. Data for chamber temperature, flow rate and CO<sub>2</sub> concentration were recorded using a micrologger (21X, Campbell Scientific, Logan, UT, USA) at 10-min intervals. A daily average of whole plant CO<sub>2</sub> assimilation was determined on a leaf area basis, taking

into account the total leaf area of the plant for each harvest. (Estimates of leaf area between harvest dates were extrapolated from harvest data). Single leaf gas exchange was determined using an open-gas-exchange system (CIRAS-1, PP Systems) under the growth conditions for the first trifoliate leaf for 3–5 plants at full expansion.

At ca 48-h intervals during the 7–9-day period, the two measured plants and three to four additional (non measured) plants were harvested and a new set of plants placed within the measurement chambers. At each harvest, plants were separated into leaves, stems and roots and were oven dried at 70°C for 48–96 h (depending on sample size). Leaf area was also measured with a leaf area meter (Model 3100, Li-Cor). Leaf area ratio (LAR), and relative growth rate (RGR) were used to calculate net assimilation rate (NAR) over the 7–9 day measurement period. LAR, RGR and NAR were determined according to Jones (1983). All remaining plants for all growth temperatures (except 40°C) were harvested 21–22 days after sowing (DAS). For the 40°C growth temperature, plants failed to develop normally and all plants were harvested at 17 DAS. The failure of the 40°C plants to produce adequate leaf area (at either CO<sub>2</sub> concentration) prevented measurement of gas exchange data for this temperature treatment.

## Results

### Enhancement of CO<sub>2</sub> assimilation

For fully expanded single leaves, the rate of CO<sub>2</sub> assimilation was significantly greater for leaves grown at 700  $\mu\text{mol mol}^{-1}$  compared to that of leaves grown at 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> at all growth temperatures (Fig. 1). At growth temperatures above 20°C, the stimulation of assimilation

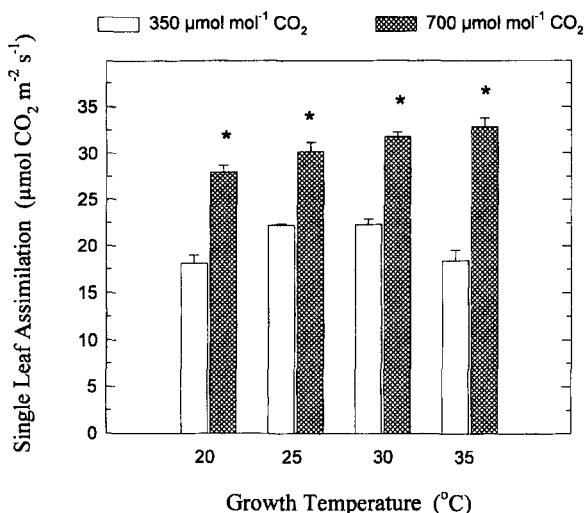


Fig. 1. Rates of single leaf assimilation of the terminal leaflet of the first trifoliate of soybean at 700  $\mu\text{mol CO}_2 \text{ mol}^{-1}$  for leaves grown at four different temperatures (20, 25, 30 and 35°C) and two CO<sub>2</sub> concentrations (350 and 700  $\mu\text{mol mol}^{-1}$ ). See Materials and method for additional details. \* Indicates a significant difference ( $P < 0.05$ ) using a Student's unpaired *t*-test. PPFD = 2000  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ,  $n = 3$ –5 plants.

at elevated CO<sub>2</sub> (relative to the ambient condition) increased with increasing temperature, with the greatest relative stimulation observed for the 35°C treatment (Fig. 1). Two-way analysis of variance indicated that the CO<sub>2</sub> by temperature interaction was significant at  $P = 0.05$ .

Measurements of whole plant assimilation early in development showed a similar enhancement by the higher CO<sub>2</sub> concentration, but this stimulation declined precipi-

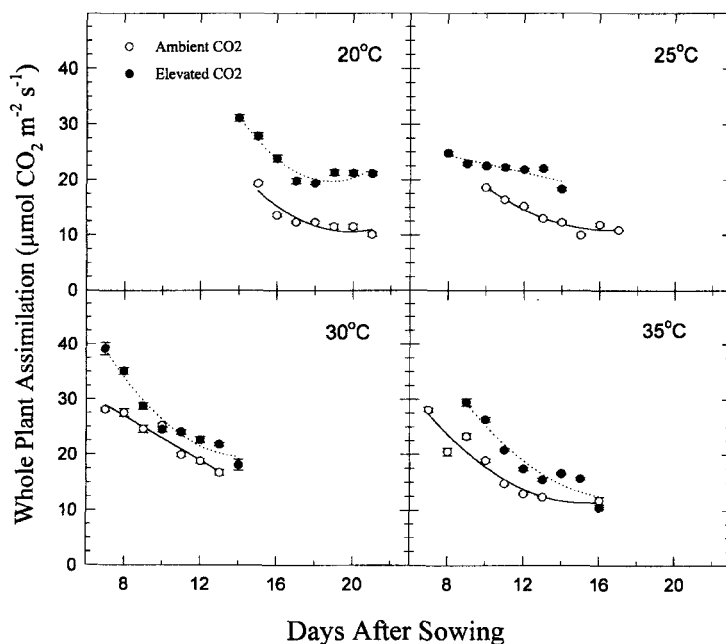


Fig. 2. Rates of whole plant assimilation calculated on a total leaf area basis for soybean grown at four different temperatures (20, 25, 30 and 35°C) and two CO<sub>2</sub> concentrations (350, [○] and 700 [●]  $\mu\text{mol mol}^{-1}$ ). Each point represents an average of 84 10-min values taken from 0800 to 2200 h. At the 30 and 35°C growth temperatures, no further stimulation of CO<sub>2</sub> assimilation was observed after 10 and 13 DAS, respectively. (Student's unpaired *t*-test).

Tab. 1. Change in whole plant assimilation ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and NAR ( $\text{g m}^{-2} \text{ day}^{-1}$ ) in soybean as a function of constant growth temperature (20, 25, 30 and 35°C) and  $\text{CO}_2$  concentration (350, 700  $\mu\text{mol mol}^{-1}$ ). \* Indicates a significant difference ( $P < 0.05$ ) as a function of  $\text{CO}_2$  using a Student's unpaired  $t$ -test.

Growth temperature	$\text{CO}_2$ concentration	Assimilation	NAR
20	350	12.9	6.8
	700	22.8*	14.7*
25	350	13.5	12.4
	700	22.1*	19.1*
30	350	22.9	15.8
	700	26.7	17.1
35	350	17.9	17.1
	700	19.4	17.6

tously at the higher growth temperature (i.e. 30 and 35°C, Fig. 2). In contrast, at the lower growth temperatures (i.e. 20 and 25°C) the enhancement of  $\text{CO}_2$  assimilation by the higher  $\text{CO}_2$  concentration persisted during the measurement period (Fig. 2). To confirm this relationship, mean daily assimilation rates were averaged over the measurement period and compared with estimated values of NAR for the same period. In both cases, similar relationships between  $\text{CO}_2$  enhancement and increasing growth temperature were observed (Tab. 1).

#### Growth enhancement

The relative enhancement of plant dry weight (roots, stems and leaves) by the higher  $\text{CO}_2$  concentration was

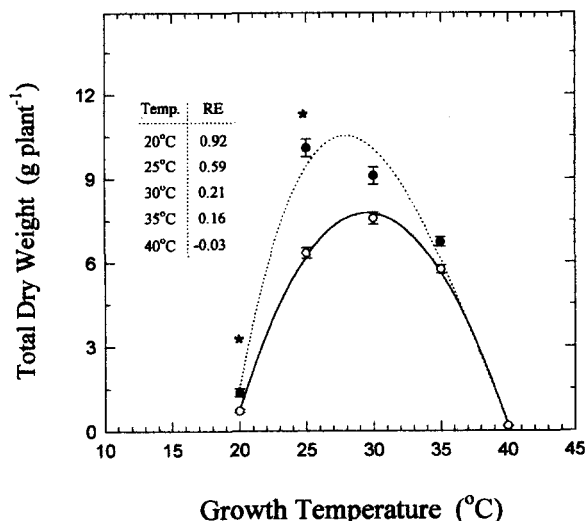


Fig. 3. Change in total dry weight (leaves, stems and roots) of soybean plants grown at five different temperatures (20, 25, 30, 35 and 40°C) and two  $\text{CO}_2$  concentrations (350 [○] and 700 [●]  $\mu\text{mol mol}^{-1}$ ) after 22 DAS (17 DAS for the 40°C). RE is the relative enhancement of growth at the elevated  $\text{CO}_2$  concentration (relative to ambient  $\text{CO}_2$ ). \* Indicates a significant effect on whole plant dry weight as a result of growth at elevated  $\text{CO}_2$  (Student's unpaired  $t$ -test).  $n=5$ .

Tab. 2. Harvest characteristics of soybean by weight ( $\text{g plant}^{-1}$ ) as a function of constant growth temperature (20, 25, 30, 35 and 40°C) and  $\text{CO}_2$  concentration (350, 700  $\mu\text{mol mol}^{-1}$ ). \* Indicates a significant difference ( $P < 0.05$ ) as a function of  $\text{CO}_2$  using a Student's unpaired  $t$ -test. All plants were harvested at 22 DAS except for the 40°C treatment which was harvested at 17 DAS.

Growth temperature	$\text{CO}_2$ concentration	Leaf weight	Stem weight	Root weight	Total weight
20	350	0.45	0.09	0.17	0.71
	700	0.78*	0.20*	0.37*	1.36*
25	350	3.26	1.30	1.79	6.35
	700	5.30*	1.62	3.08*	10.10*
30	350	4.32	1.34	1.93	7.60
	700	5.26*	1.47	2.38	9.11
35	350	3.23	1.37	1.26	5.76
	700	4.15*	1.19	1.43	6.76
40	350	0.12	0.02	0.03	0.17
	700	0.12	0.02	0.02	0.16

reduced or eliminated as growth temperatures increased (Fig. 3). (Relative enhancement was determined at the final harvest [22 DAS], and calculated as  $(E-A)/A$ , where E and A stand for the elevated and ambient  $\text{CO}_2$  treatments, respectively). The greatest relative enhancement was observed at 20°C (0.92) with no significant enhancement from higher  $\text{CO}_2$  observed at temperatures above 30°C. Overall during this period, growth at elevated  $\text{CO}_2$  shifted the optimal growth temperature downward ca 2°C relative to the ambient  $\text{CO}_2$  condition as determined by the maximum value of the fitted curve (Fig. 3).

With respect to growth parameters of individual organs, root growth showed the greatest stimulation at elevated  $\text{CO}_2$  at the lower growth temperatures with significant increases noted in root/shoot (R/S) (Tab. 2). Significant increases in stem weight were only observed with elevated  $\text{CO}_2$  at 20°C. Interestingly, however, a significant stimulation in leaf weight was observed at elevated  $\text{CO}_2$  for all growth temperatures.

The relationship between temperature and  $\text{CO}_2$  for leaf area was opposite to that observed for whole plant  $\text{CO}_2$  assimilation rate and growth stimulation (Fig. 4). That is, elevated  $\text{CO}_2$  increased leaf area more at higher growth temperatures (Fig. 4). Estimates of leaf area index (LAI) determined using the surface area of individual pots (ca 190  $\text{cm}^2$ ) showed an approximate doubling of LAI at 35°C with elevated  $\text{CO}_2$  (3.8 vs 6.9) at 21 DAS. When whole plant  $\text{CO}_2$  assimilation rate was plotted as a function of leaf area, the relationship between  $\text{CO}_2$  and growth temperature was similar to that observed in Fig. 2 (Fig. 5). That is, as total leaf area increased, the stimulation in  $\text{CO}_2$  assimilation rate (at equivalent total leaf area) decreased at the warmer, but not the cooler growth temperature (Fig. 5).

#### Discussion

At the single leaf level, stimulation of  $\text{CO}_2$  assimilation at the higher  $\text{CO}_2$  concentration was observed at all

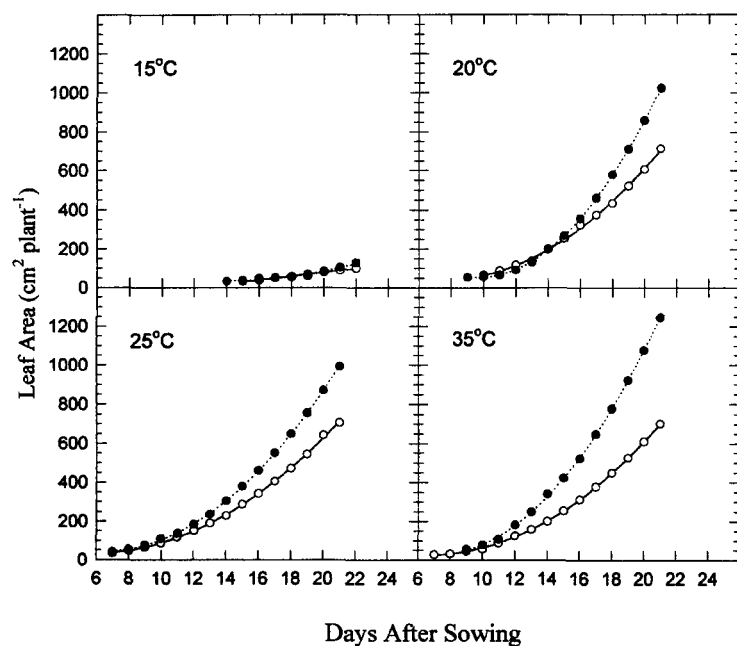


Fig. 4. Leaf area for soybean grown at four different temperatures (20, 25, 30 and 35°C) and two CO<sub>2</sub> concentrations (350 [○] and 700 [●] µmol mol<sup>-1</sup>) as a function of time. Estimated curves were determined based on four harvests of leaf area (n = 5 plants for each harvest) at different DAS for each growth temperature (up to 35°C) and CO<sub>2</sub> concentration. All estimated curves had a R<sup>2</sup> value > 0.98.

growth temperatures during the measurement period. Over the range from 25 to 35°C (i.e. at optimal growth), the relative stimulation of CO<sub>2</sub> assimilation rate increased from 36 to 72%. This is consistent with the theoretical predictions for increasing temperature and elevated CO<sub>2</sub> (e.g. Idso et al. 1987). That is, since photorespiratory carbon loss increases with temperature and in-

creasing CO<sub>2</sub> concentration reduces photorespiratory loss (thus increasing net photosynthesis), elevated CO<sub>2</sub> should stimulate CO<sub>2</sub> assimilation more as temperature rises (cf. Long 1991).

However, the same interaction between temperature and CO<sub>2</sub> was not observed for whole plant CO<sub>2</sub> assimilation during this same period. At the whole plant level,

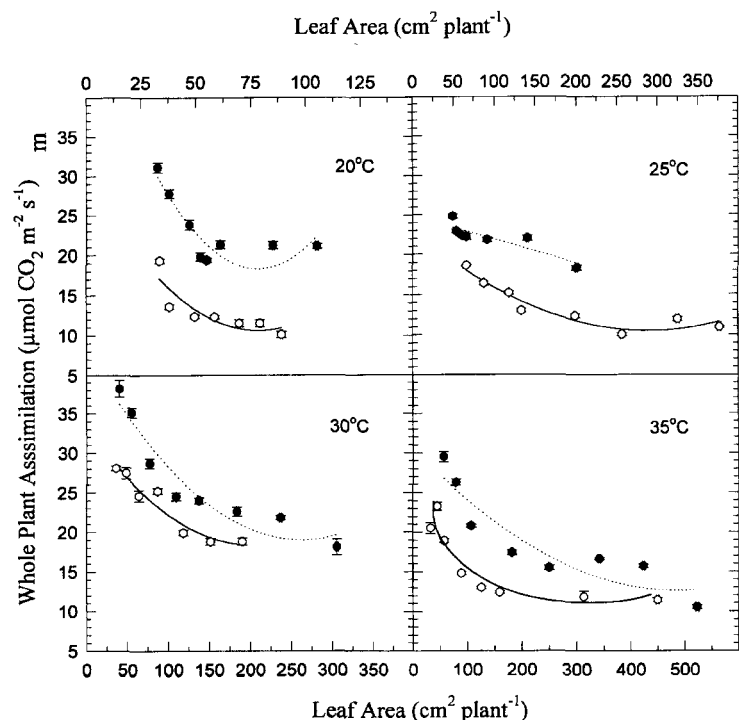


Fig. 5. Rates of whole plant CO<sub>2</sub> assimilation calculated on a total leaf area basis for soybean grown at four different temperatures (20, 25, 30 and 35°C) and two CO<sub>2</sub> concentrations (350 [○] and 700 [●] µmol mol<sup>-1</sup>) as a function of total leaf area per plant. Assimilation was determined over a 7–9-day period. Additional details are given in Materials and methods. Symbols and relationships are described in Fig. 2.

the relative stimulation of both CO<sub>2</sub> assimilation rates and growth at elevated CO<sub>2</sub> declined as growth temperature increased. In fact, the enhancement of CO<sub>2</sub> assimilation rate by elevated CO<sub>2</sub> concentration was not observed by 14 DAS at both the 30 and 35°C temperature treatments. Given the results obtained for single leaf assimilation rates, why would growth temperature influence the degree of stimulation at elevated CO<sub>2</sub> differently for the whole plant? Plants showed no evidence of water stress or nutrient deficiency at growth temperatures up to 35°C for either CO<sub>2</sub> concentration.

One potential difference in the response of single leaf and whole plant assimilation rates may be the light environment created by self-shading. The CO<sub>2</sub> effect on self-shading varied with temperature. At 35°C for example, the leaf area for the elevated CO<sub>2</sub> treatment was approximately twice that at lower CO<sub>2</sub> at 22 DAS, while no CO<sub>2</sub> effect on leaf area occurred for the 20°C temperature treatment.

When plants were grown at 25°C then placed in a 35°C environment just prior to the initiation of whole plant photosynthetic measurements (i.e. unfolding of first trifoliate), there were no differences in leaf area between ambient and elevated CO<sub>2</sub> during the measurement time (Fig. 6). Under these conditions, continued stimulation of CO<sub>2</sub> assimilation at the higher CO<sub>2</sub> concentration for

whole plants was observed for the entire measurement period (i.e. 8 to 14 DAS) (Fig. 6). This suggests that increased leaf area with elevated CO<sub>2</sub> at higher temperatures led to a decrease in the relative enhancement of CO<sub>2</sub> assimilation rate at the whole plant level.

However, it is not clear why this should occur. Because increasing CO<sub>2</sub> concentration reduces photorespiration and lowers the light compensation point (Long 1991), net stimulation of CO<sub>2</sub> assimilation at elevated CO<sub>2</sub> should still occur even at low PPFDs caused by self-shading. In fact, the relative stimulation of single leaf assimilation rate by elevated CO<sub>2</sub> may be much higher at low PPFD (cf. Ziska et al. 1990). Furthermore, the relative stimulation of assimilation by elevated CO<sub>2</sub> at low PPFD also increases strongly with temperature (Long 1991). In the current study, therefore, stimulation of whole plant assimilation should have continued at elevated CO<sub>2</sub> as temperature increased, even if the amount of self-shading increased as well. This would have been evident by higher whole plant assimilation rates at elevated compared to ambient CO<sub>2</sub> at equal total leaf areas (i.e. same amount of self-shading). However, in the current study, smaller differences in whole plant assimilation between elevated and ambient CO<sub>2</sub> treatments at equivalent total leaf areas were observed with increasing growth temperature and at high leaf area (i.e. Fig. 5). This sug-

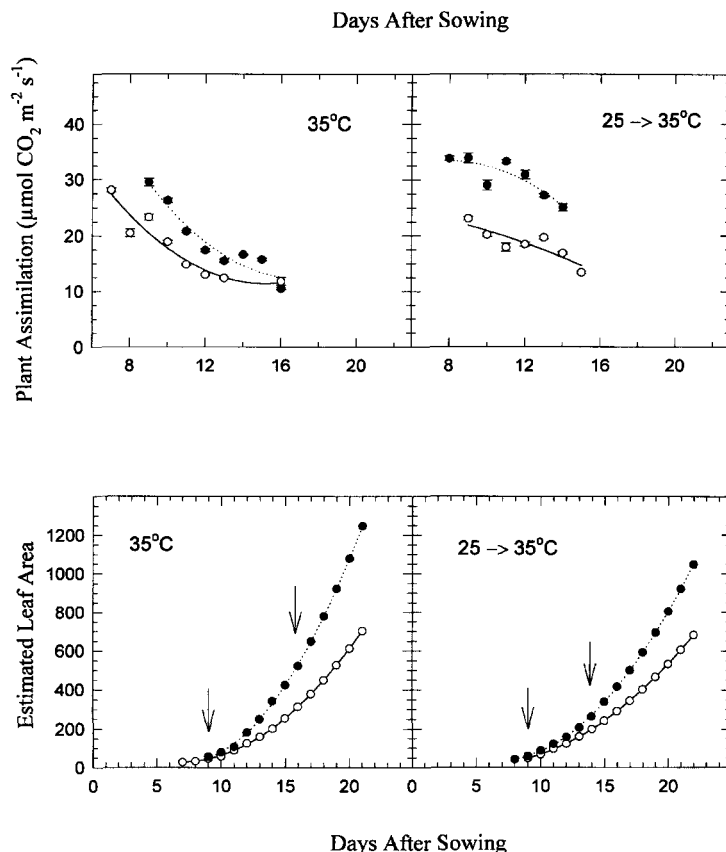


Fig. 6. Comparison of whole plant CO<sub>2</sub> assimilation and estimated leaf area for the 35°C temperature treatment (taken from Figs 2 and 4, respectively) with plants exposed to a growth temperature of 25°C prior to measurement of whole plant photosynthesis and estimated leaf area. No significant differences in leaf area were observed between ambient and elevated CO<sub>2</sub> concentration for the 25 to 35°C switched treatments during the measurement of whole plant photosynthesis (shown by arrows in figure). Symbols are given in Fig. 2.

gests instead, that shaded leaves had less relative stimulation by elevated CO<sub>2</sub> at warmer temperatures.

The mechanism by which assimilation in shaded leaves would become insensitive to higher CO<sub>2</sub> concentrations at high growth temperatures is unclear. Sicher et al. (1995) demonstrated that long-term growth at elevated CO<sub>2</sub> reduced the quantum yield of photosynthesis. It is not known, however, if the acclimation of quantum yield at high CO<sub>2</sub> could be temperature dependent in soybean. Bunce (1997) found that the amount of photosynthetic acclimation to elevated CO<sub>2</sub> varied with the PPFD used to measure photosynthesis. We cannot rule out the possibility that a similar phenomenon occurred in this study.

In addition to providing a partial explanation for the temperature insensitivity of soybean photosynthesis at the whole plant vs the single leaf at elevated CO<sub>2</sub>, the current experiment also suggests the importance of PPFD on stimulation of CO<sub>2</sub> assimilation in soybean. It is evident in the current experiment that the amount of self-shading experienced by the whole plant could limit its photosynthetic response to elevated CO<sub>2</sub>. This suggests that the degree of photosynthetic stimulation to elevated CO<sub>2</sub> could differ depending on the PPFD; with the amount of PPFD experienced by the whole plant determined, in turn, by the growth temperature. (A similar result might also be expected for whole canopies, with self-shading plus shading of all plants).

If increased temperature influences leaf area and the degree of shading, predictions based on known carboxylation kinetics at the leaf level may be inadequate to predict the response of CO<sub>2</sub> assimilation to concurrent increases in temperature and CO<sub>2</sub> for whole plants or canopies of soybean.

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## References

- Acock, B., Acock, M. C. & Pasternak, D. 1990. Interactions of CO<sub>2</sub> enrichment and temperature on carbohydrate production and accumulation in muskmelon leaves. – *J. Am. Soc. Hortic. Sci.* 115: 525–529.
- Baker, J. T. & Allen, L. H. Jr. 1993. Contrasting crop species response to CO<sub>2</sub> and temperature: rice, soybean and citrus. – *Vegetatio* 104/105: 239–260.
- Bunce, J. A. 1997. Variation in growth stimulation by elevated carbon dioxide in seedlings of some C<sub>3</sub> crop and weed species. – *Global Change Biol.* (In press).
- & Ward, D. A. 1986. Source-sink balance as a factor in photosynthetic acclimation. – *In Biological Control of Photosynthesis* (R. Marcelle, ed.), pp. 241–250. Martinus Nijhoff Publishers, Dordrecht. ISBN 90-247-3287-5.
- Campbell, W. J., Allen, L. H. Jr & Bowes, G. 1990. Response of soybean canopy photosynthesis to CO<sub>2</sub> concentration, light and temperature. – *J. Exp. Bot.* 41: 427–433.
- Cure, J. D. & Acock, B. 1986. Crop responses to carbon dioxide doubling: A literature survey. – *Agric. For. Meteorol.* 38: 127–145.
- Eamus, D., Berryman, C. A. & Duff, G. A. 1993. Assimilation, stomatal conductance, specific leaf area and chlorophyll responses to elevated CO<sub>2</sub> of *Maranthos corymbosa*, a tropical monsoon rain forest species. – *Aust. J. Plant Physiol.* 20: 741–755.
- Idso, S. B., Kimball, B. A., Anderson, M. G. & Mauney, J. R. 1987. Effects of atmospheric CO<sub>2</sub> enrichment on plant growth: The interactive role of air temperature. – *Agric. Ecosyst. Environ.* 20: 1–10.
- Jones, H. G. 1983. Measurement and analysis of CO<sub>2</sub> exchange. – *In Plants and Microclimate* (H. G. Jones, ed.), pp. 140–150. Cambridge University Press, Cambridge. ISBN 0-521-27016-2.
- Jones, P., Allen, L. H. Jr & Jones, J. W. 1985. Responses of soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO<sub>2</sub> environments. – *Agron. J.* 77: 242–249.
- Long, S. P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: Has its importance been underestimated? – *Plant Cell Environ.* 14: 729–739.
- Mearns, L. O., Katz, R. W. & Schneider, S. H. 1984. Extreme high temperature events – changes in their probabilities with changes in mean temperature. – *J. Climat. Appl. Meteorol.* 23: 1601–1613.
- Potvin, C. 1994. Interactive effects of temperature and atmospheric CO<sub>2</sub> on physiology and growth. – *In Plant Responses to the Gaseous Environment* (R. G. Alscher and A. R. Wellburn, eds), pp. 39–54. Chapman and Hall, London. ISBN 0-412-58170-1.
- Robinson, J. M. 1984. Photosynthetic carbon metabolism in leaves and isolated chloroplasts from spinach plants grown under short and intermediate photosynthetic periods. – *Plant Physiol.* 75: 397–409.
- Sage, R. F. 1994. Acclimation of photosynthesis to increasing atmospheric CO<sub>2</sub>: The gas exchange perspective. – *Photosynth. Res.* 39: 351–368.
- & Sharkey, T. D. 1987. The effect of temperature on the occurrence of O<sub>2</sub> and CO<sub>2</sub> insensitive photosynthesis in field grown plants. – *Plant Physiol.* 84: 658–664.
- Schlesinger, M. E. 1986. Equilibrium and transient climatic warming induced by increased atmospheric CO<sub>2</sub>. – *Clim. Dyn.* 1: 35–51.
- Sicher, R. C., Kremer, D. F. & Rodermeil, S. R. 1994. Photosynthetic acclimation to elevated CO<sub>2</sub> occurs in transformed tobacco with decreased ribulose-1,5 biphosphate carboxylase/oxygenase content. – *Plant Physiol.* 104: 409–415.
- , Kremer, D. F. & Bunce, J. A. 1995. Photosynthetic acclimation and photosynthate partitioning in soybean leaves in response to carbon dioxide enrichment. – *Photosynth. Res.* 46: 409–417.
- Sionit, N., Strain, B. R. & Flint, E. P. 1987. Interaction of temperature and CO<sub>2</sub> enrichment on soybean: Photosynthesis and seed yield. – *Can. J. Plant Sci.* 67: 629–636.
- Woodrow, I. E. 1994. Optimal acclimation of the C<sub>3</sub> photosynthetic system under enhanced CO<sub>2</sub>. – *Photosynth. Res.* 39: 401–412.
- Wulff, R. D. & Strain, B. R. 1982. Effects of CO<sub>2</sub> enrichment on growth and photosynthesis in *Desmodium paniculatum*. – *Can. J. Bot.* 60: 1084–1091.
- Ziska, L. H. & Bunce, J. A. 1995. Growth and photosynthetic response of three soybean cultivars to simultaneous increases in growth temperature and CO<sub>2</sub>. – *Physiol. Plant.* 94: 575–584.
- , Drake, B. G. & Chamberlain, S. 1990. Long-term photosynthetic response in single leaves of a C<sub>3</sub> and C<sub>4</sub> salt marsh species grown at elevated atmospheric CO<sub>2</sub> in situ. – *Oecologia* 83: 469–472.

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